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THE AMERICAN NATURALIST.

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ON THE EXTINCT DOGS OF NORTH AMERICA.

BY PROFESSOR E. D. COPE.

THE family of the Canidæ occupies in the order of the Carnivora, a position intermediate between the generalized forms, as the raccoons, and the highest or specialized forms, as the cats. While its sectorial or flesh teeth are well developed, the primitive tuberculars remain in the jaws behind them, frequently to the full number in the superior jaw, and in rarely less than the full number in the lower jaw. The sectorials themselves are of inferior type, for the superior generally lacks the anterior lobe, and the inferior has a large heel, which is frequently tubercular. The number of the toes, generally 5-4, is smaller than in the lower types, but not so much reduced as in the hyænas, where they are but four on all the feet. In spite of the intermediate position of the Canidæ in general structure, they display superiority to all of the other families in the character of the brain. There are four longitudinal convolutions of the cerebral hemispheres, while the other families have but three; though in some of them (civets, cats), the inferior (Sylvian) convolution is fissured at the ends.¹ This character of the dogs is in some degree parallel to that of man, whose great brain superiority is associated with general inferiority in the osseous and digestive systems.

The range of variation in the family Canidæ, is found in the number of the tubercular teeth, and of the tubercles of the sectorials, and in an occasional reduction in the number of the pre-

¹ For the characters of the families of Carnivora, see *Proceed. Amer. Philos. Soc.*, 1882, p. 471.

molars.¹ Thus in *Megalotis* the true molars number $\frac{3}{4}$, and in *Icticyon*, at the other end of the series, $\frac{2}{3}$. The genus which adds to this reduction a further diminution in the number of premolars, *Dysodus*,² is only known in a domesticated condition.

The Canidæ probably first appeared in the Upper Eocene epoch. Cuvier described a *Canis parisiensis* from the Gypsum of Montmartre, but it is not as yet known whether it belongs to the restricted genus *Canis* or not. From the Phosphorites of Central France come the *Canis filholi* Mun. Chal., and *Brachycyon gaudryi* Filhol. The phosphatic deposit in which these species occur, contains fossils of both Eocene and Miocene age, so that the position of these Canidæ is yet uncertain. In North America no undoubted species of Canidæ has been found in beds older than Oligocene or oldest Miocene; that is below the White River formation. They are most abundant in the John Day epoch, or Middle Miocene, and are not rare in the Upper Miocene, or Loup Fork epoch. Species accompany the Pliocene fauna everywhere.

I give the following analysis of the extinct genera found in North America:

- I. Molar formula $\frac{4}{3} \frac{3}{3}$.
Humerus with epitrochlear foramen.....*Amphicyon*.
- II. Molar formula $\frac{4}{4} \frac{3}{3}$.
 - a. No anterior lobe of superior sectorial.
 - β. Humerus with epitrochlear foramen.
Inferior sectorial with heel trenchant.....*Temnocyon*.
Inferior sectorial with heel basin-shaped.....*Galecyon*.
ββ. Humerus without epitrochlear foramen.
Inferior sectorial with heel basin-shaped.....*Canis*.
 - aa. An anterior lobe of superior sectorial.
Heel of lower sectorial basin-shaped; no epitrochlear foramen.....*Ælurodon*.
- III. Molar formula $\frac{3}{3} \frac{2}{2}$.
Heel of inferior sectorial trenchant; premolars lobed posteriorly.....*Enhydrocyon*.
Heel of inferior sectorial basin-shaped; superior molars unknown.....*Tomarctus*.
- IV. Molar formula $\frac{4}{4} \frac{1}{2}$.
Heel of inferior sectorial basin-shaped; internal cusp present.....*Oligobunis*.
- V. Molar formula $\frac{3}{3} \frac{1}{1}$.
Premolars lobed; first inferior two-rooted.....*Hyænocyon*.

To these genera I refer twenty-five species of the American Miocenes.

¹ For the genera of Canidæ, see Proceeds, Acad. Nat. Sci. Philada., July, 1879.

² See on this genus AMERICAN NATURALIST, 1881, p. 233, and July, 1879.

AMPHICYON Lartet.

Much is yet to be desired in the elucidation of the characters of this genus, especially of the American forms, which are less abundant and of smaller size than those of Europe. The typical species, *Amphicyon major* Blv., was the largest, equaling a bear in size. It is derived from the Miocene of Sansan, France, and a smaller form of it is found, according to Pomel, at San Gerand-le-Puy. Other species are derived from the latter locality, and all are typical of the Miocene formation in Europe. In the "Mio-pliocene" of India, a single species has been discovered, the *A. palæindicus* of Lydekker. The species occur in the Lower and Middle Miocene of North America, the largest of which about equals the wolf in size. On account of the large development of the inferior tubercular teeth, I have suspected that the *Canis ursinus* Cope, from the Loup Fork group of New Mexico, would prove to be an Amphicyon. If so, it is the only representative of this genus in our Upper Miocene.

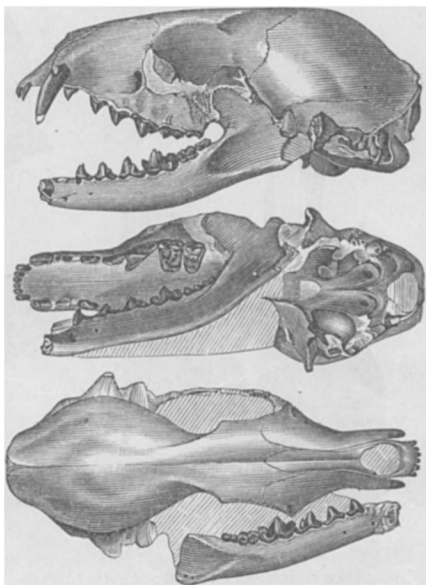


FIG. 1.—*Amphicyon cuspidatus* Cope, with the last superior molar lost; one-half natural size. Three views of skull. From the John Day beds of Oregon. Original.

The three American species differ as follows: The *A. cuspidatus*¹ is small, not exceeding the kit-fox in dimensions. The *A. hartshornianus* is about the size of the coyote, and has rather small tubercular molars, especially of the lower series. The *A. vetus* Leidy, is a little larger, but has the tubercular molars disproportionately larger than those of the *A. hartshornianus*.

TEMNOCYON Cope.

The characters on which I rely at present for the discrimination of this genus from *Canis* are two. The first is the presence of a cutting edge on the superior face of the heel of the inferior sec-

¹ *Amphicyon entoptychi* is the same.

torial, in place of a double row of tubercles surrounding a basin. When well developed these characters present a broad contrast, but indications of transitional forms are not wanting. Thus, in some extinct Canes the internal crest of the heel is less elevated than the external, which is the homologue of the single crest of

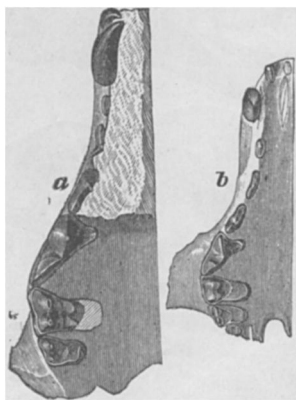


Fig. 2.

FIG. 2.—*a*, *Temnocyon altigenis* Cope, superior teeth of right side. From the John Day epoch of Oregon; *b*, *Amphicyon hartshornianus* Cope, superior teeth of right side; from White River epoch of Colorado. Both figures one-half natural size. Original.

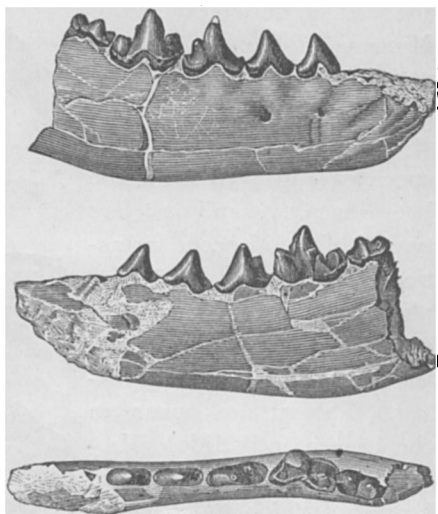


Fig. 3.

FIG. 3.—*Temnocyon altigenis* Cope, part of right mandibular ramus, one-half natural size; viewed from without, within, and above. Original. From Report U. S. Geol. Survey Terrs., Vol. iv.

Temnocyon, and in some specimens of *Temnocyon coryphæus* there is a cingulum on the inner side of the median keel, which represents the internal crest of *Canis*. Secondly, the epitrochlear foramen of the humerus, a character common to all of our Lower Miocene Canidæ yet known.

The keel of the sectorial, which defines this genus, is simply a repetition on that tooth of the keel which belongs to the posterior premolar teeth of many Carnivora. I find resemblances in such Eocene forms as *Mesonyx* and *Palæonyctis*. Among recent Canidæ it is apparently known only in the genus *Icticyon*, and is very rare in other groups. The *Cynodictis crassirostris* Filhol, from the French Phosphorites, strongly resembles the species of *Temnocyon* in generic characters, and the *Amphicyon incertus*, also French, may turn out to belong to this genus.

Three American species certainly belong to *Temnocyon*. These differ in size, proportions and the forms of the superior tubercular molars. The largest, and type of the genus, the *T. altigenis* (Fig. 3), is as large as a wolf. *T. wallovianus* Cope, has a shorter and wider head. *T. coryphæus* (Fig. 4) is as large as the coyote, and was very abundant during the John Day epoch in Oregon. *T. josephi* Cope, provisionally referred to this genus, is still smaller, and has a narrower muzzle and wider face. All the species differ from the true dogs in their shorter muzzle and longer and nar-

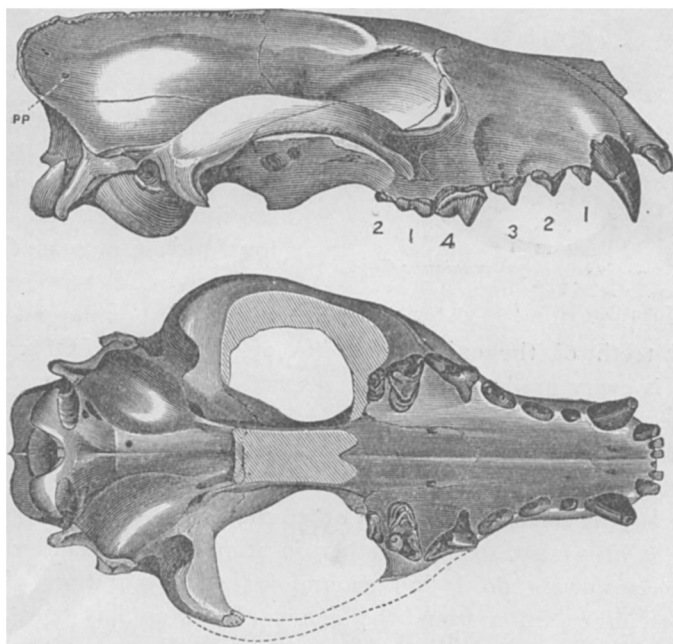


FIG. 4.—*Temnocyon coryphæus* Cope, more than one-half natural size. From John Day epoch, Oregon. Original. From Report U. S. Geol. Survey Terrs., F. V. Hayden, Vol. iv. The numbers indicate the premolars and molars. No. 4 is the sectorial.

rower brain-case, in these points resembling the civets. They come from the John Day epoch, and probably also the White River beds of Nebraska.

GALECYNUS OWEN.

This genus, which is abundantly represented by species and individuals, existed during the Upper Eocene (the Phosphorites), and Miocene epochs in Europe, and also during the White River, or Oligocene, in North America. As the structure of the feet of

the numerous species from these epochs is not yet known, and, therefore some doubt as to their correct generic reference may still exist, I only regard the genus as a certain inhabitant of North America during the John Day, or Middle Miocene, epoch. This is indicated by the *Galecynus geismarianus*, where the number of the toes on the posterior foot has been ascertained (Fig. 6).

All the species of the genus from Eocene and Lower Miocene

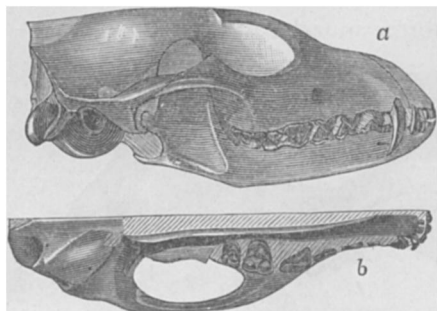


FIG. 5.—*Galecynus geismarianus* Cope, one-half nat. size, skull from side and below. From John Day beds, Oregon. Original.

beds, as well as most of those of the Loup Fork epoch, are characterized by the relatively small size of their sectorial teeth.¹ In this they resemble the Amphicyons, Temnocyons and other forms of Canidæ of the same period, and differ from such Canes as *C. ursinus* and *C. haydeni*, which display the enlarged sectorial

teeth of the existing species of the genus. Of course there is every gradation in this respect between the two types. In the older species the internal tubercle of the inferior sectorial tooth is more largely developed than in the latter ones, thus approaching some of the species of Viverridæ, where it is still more largely developed. As in other characters, there are gradations in this also, so that neither in it nor in the relative size of the sectorials do I find ground for the separation of the species in question from the genus *Canis*, as has been proposed in the case of some of the species in Europe. Through the kindness of M. Filhol, I possess jaws of a number of the species found by himself and others in the Phosphorites of Central France, including the *Canis velaunus*, the type of the genus *Cynodon* of Aymard. These agree very nearly with the species of dogs from the American Miocene beds as to generic characters. Professor Owen proposed to distinguish the genus *Galecynus* on account of the greater length of the pollex as compared with that found in the existing species of *Canis*. This character appears to me to be of an unsatisfactory nature, owing to the fact

¹ See Bulletin U. S. Geol. Survey of the Terrs., F. V. Hayden, Vol. vi, 1881, p. 180.

that gradations in the length of a digit are difficult to express with precision in other than a specific sense; and the gradations may certainly be expected to occur.

I find in the *G. geismarianus* a character which separates the genus from *Canis*, viz., the presence of the epitrochlear foramen of the humerus. In this point it agrees with *Amphicyon* and *Temnocyon*. I arrange cotemporary and generally similar species under the same generic head, as the most reasonable course in the absence of direct evidence.

I know four species of *Galecynus* from American localities. These are, in the order of size, beginning with the largest. *G.*

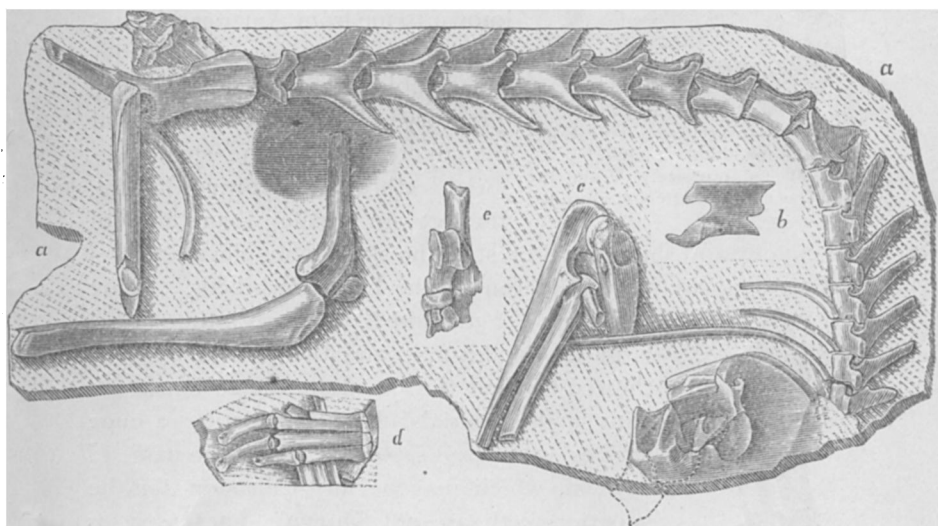


FIG. 6.—Part of skeleton of one individual of *Galecynus geismarianus*, one-half nat. size; from the John Day bed of Oregon; *a*, vertebral column with pelvis; *b*, axis vertebra; *c*, elbow, showing epitrochlear foramen; *d*, metatarsus and phalanges; *e*, tarsus, showing grooved astragalus. Original.

geismarianus Cope (Figs. 5–6), *G. latidens* Cope, *G. gregarius* Cope, and *G. lemur* Cope (Fig. 7). Three of these are confined to the John Day Miocene, while the *G. gregarius* is abundant in the White River formation of Colorado and Dakota. The *G. geismarianus* (Figs. 5–6), is a little smaller than the gray fox (*Vulpes virginianus*), and had a more civet-like form. That is, the body was relatively longer and the limbs shorter. The *G. lemur* (Fig. 7) is remarkable for its very large orbits and otic bullæ. These indicate large eyes and large ears, and render it probable that the animal was nocturnal in its habits. These, with its

short, sharp nose, must have given it a physiognomy something like that of the existing fennec of Nubia.

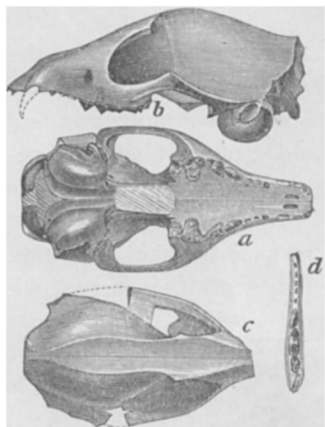


FIG. 7.—*Galecynus lemur* Cope, skull and mandibular ramus (Fig. *d*), one half natural size. From the John Day epoch of Oregon. Original.

Filhol has described seventeen species of this genus from the Phosphorites of France, and has given several generic names to groups which do not seem to be distinct from it.

CANIS Linn.

The oldest species of true dog known to me from American formations is the *C. brachypus* Cope, from the Ticholeptus epoch of Wyoming Territory. It is about the size of the coyote, but has the small sectorial teeth of all primitive Canidæ. Its feet are smaller than those of the coyote, and the sagittal crest of the skull more elevated.

True dogs are more numerous in the Loup Fork beds. Leidy describes *C. vafer* and *C. temerarius*, the first as large as the kit-fox; and the second between the red fox and the coyote in dimensions, both with small sectorials. He also describes a huge species, with large sectorials, under the name *C. haydeni*, which may be an *Ælurodon*, for the superior teeth are not known. These species are from Nebraska. Another large species is the *C. ursinus* Cope, from New Mexico. It has not only large sectorials but large inferior tuberculars below, which arouses the suspicion that when the superior dentition is obtained, it will prove to be an *Amphicyon*. The form of the mandible is very peculiar.



FIG. 8.—*a*, astragalus of *Canis brachypus*; *b*, right astragalus and calcaneum of *Ælurodon saurus*; *c*, three left metatarsals of do.; all three-eighths nat.size. Original.

Canis lupus (the wolf) and *C. latrans* (the coyote) are found in the Pliocene or Equus, beds. From these species many of the domesticated dogs have been derived.

TOMARCTUS Cope.

One species known from the Loup Fork beds

of Colorado. It is uncertain whether this genus has two or three premolars. Should it have three it must be compared with the *Brachycyon* of Filhol. But the inferior sectorial tooth of that genus is as yet unknown. In *Tomarctus* it is like that of *Canis* and *Ælurodon*. The *T. brevirostris* has teeth as large as those of a coyote, but has the lower jaw shorter and more slender.

ÆLURODON Leidy.

Dr. Leidy described an *Ælurodon ferox*, whose affinities he did not determine, but which he thought to combine characters of

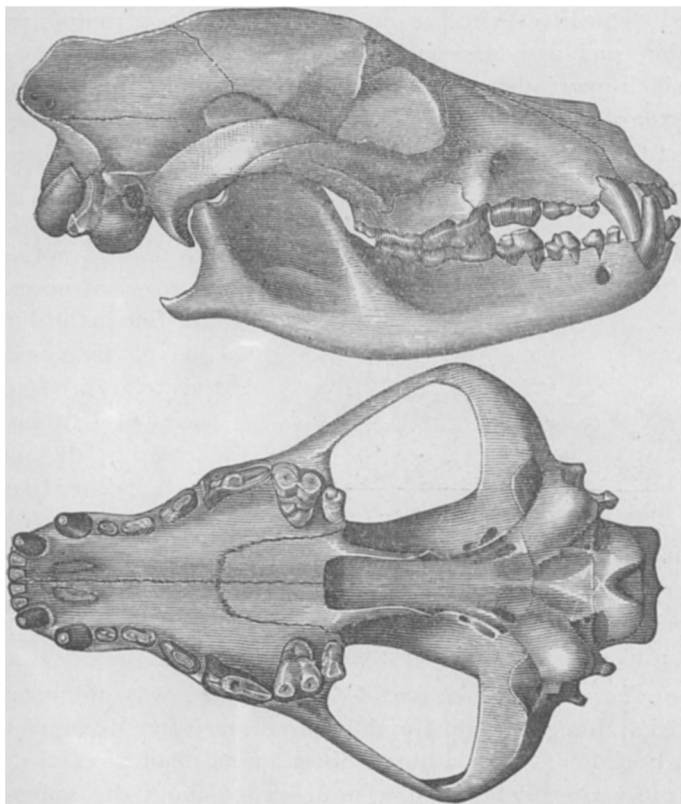


FIG. 9.—*Ælurodon sævus* Leidy, skull three-eighths nat. size. From the Loup Fork beds of Nebraska. Original.

dogs and cats. I have proven¹ by material in my possession, that the *Ælurodon ferox* and the *Canis sævus* Leidy, are the same species. The genus *Ælurodon* must be referred to the *Canidæ*, and

¹ Bulletin U. S. Geolog. Survey Terrs., vi, 1881, p. 387.

distinguished from *Canis* proper, only by the presence of an anterior cutting lobe of the superior sectorial tooth, the character on which Dr. Leidy originally proposed it. There are three species of the genus known to me, the *Æ. sævus*, *Æ. wheelerianus* (*Canis* Cope) and a smaller one which I called *Æ. hyænoides*. The character of the superior sectorial tooth above mentioned is as much like that of *Hyæna* as *Felis*, and the entire sectorial tooth in the *Æ. hyænoides* is much like that of the former genus. In all three species the premolars are very robust, as though to aid the sectorials in crushing bones, as they do in the hyænas, and which may indicate five digits in the anterior foot, the general character of the *Canidæ*, and not as in the *Hyænidæ*. I nevertheless suspect that this genus is the ancestor of the *Hyænidæ*, through the intermediate forms, *Ictitherium* and *Hyænictis*. According to Gaudry, *Ictitherium* has the same number of digits as the *Canidæ*, and the same dental characters as *Ælurodon*, excepting in the absence of the last inferior molar. He shows a successive

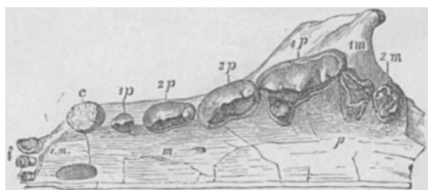


FIG. 10.—Superior dental series of *Ictitherium robustum*, two-thirds nat. size. From the Miocene of Pikermi, Greece. After Gaudry.

reduction in the dimensions of the superior true molars in the three species of *Ictitherium*, followed by the loss of the second in *Hyænictis*. I have followed Gaudry in placing the former genus in the series of *Epimycterous Carnivora* near the *Viverridæ*; but that division was largely derived from the *Hypomycterous* division, to which the *Canidæ* belong.

The *Ælurodon wheelerianus* Cope (Fig. 11), was abundant in Nebraska, though originally discovered in New Mexico in the Loup Fork beds. It is a more robust animal than *Æ. sævus*, and differs in various details. The skull was of about the same size, viz., rather shorter, but stouter than that of the *Canis lupus*. The *Æ. sævus* was equally abundant in Nebraska (Fig. 9). With the *Æ. wheelerianus* it probably performed the function of a scavenger, devouring the remains of the antelopes and small camels of the Loup Fork epoch. The *Æ. hyænoides* is a smaller species with some peculiarities of its own, from Southern Nebraska.

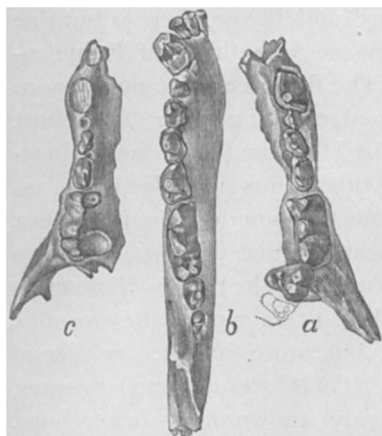


FIG. 11.—Jaws of *Aelurodon*s, three-eighths natural size. *a-b*, *A. wheeleri*-*anus* Cope, upper and lower dental series. *c*, *A. hyenoides* Cope, superior series lacking the last true molar. All three-eighths nat. size. From Loup Fork beds of Southern Nebraska. Original.

ENHYDROCYON Cope.

This genus is represented by a single rather large species, the *E. stenocephalus* Cope. The general form of the skull is that of *Temnocyon*, but the shortening of the muzzle is carried so far as to leave space for only three superior premolars. These have posterior lobes as in *Canis*, and the first is two-rooted. The muzzle is broad and flat above, and the brain-case is long and narrow. The general form of the skull would be that of an otter, but for the presence of a high sagittal crest (Fig. 12). Whether or not it is the ancestral source

of the otters, cannot yet be ascertained. Its appearance sug-

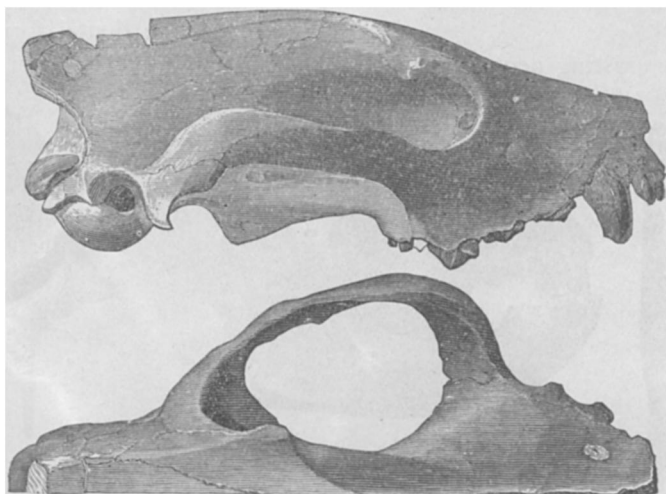


FIG. 12.—*Enhydrocyon stenocephalus*, skull, two views, one-half natural size. From the John Day beds of Oregon. Original.

gests an aquatic habit. Were the muzzle of similar proportions, the skull would be as large as that of a wolf.

HYÆNOCYON Cope.

The dental series is still more reduced in this genus than in the

last, for with three premolars above and below, there is but one true molar above. The premolars are like those of *Enhydro-*



FIG. 13.—*a*, *Enhydrocyon sten-ocephalus*, part of mandible from above; *b*, do., part of maxillary from below; *c*, *Hyanocyon basilatus*, part of mandible from above; *d*, *Hyanocyon sectorius*, maxillary bone from below. All three-eighths nat. size, and from the John Day beds, Oregon. Original.

cyon. The flesh teeth are much more developed, equaling those of the most specialized Canidæ. The family location of this genus is indeed not assured, but the superior true molar is a good deal like that of the Canidæ, so far as known. The type is *H. sectorius* Cope (Fig. 13), a species the size of a coyote, but more robust. A second species, *H. basilatus* (Fig. 13) is larger, and is only known from lower jaws. These species, are from the John Day beds of Oregon, and are the most formidable Canidæ of that period, though they do not appear to have been abundant.

OLIGOBUNIS Cope.

This genus has the dental formula of the existing neotropical genus *Icticyon*, but differs from it in

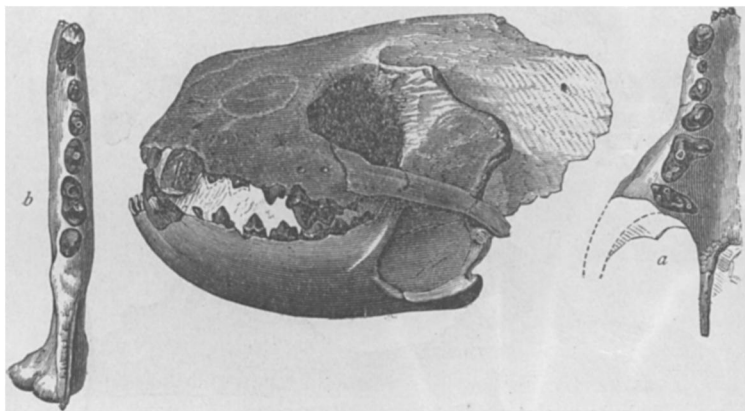


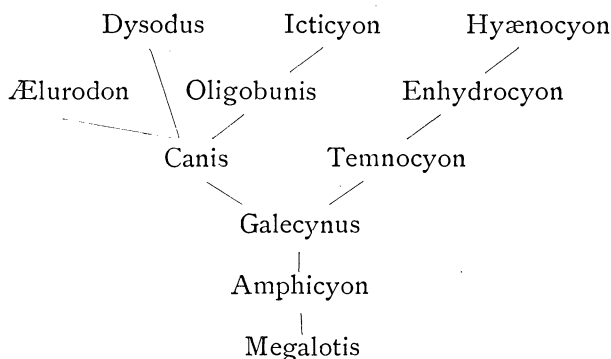
FIG. 14.—*Oligobunis crassivultus* Cope, one-half natural size. *a*, right maxillary bone with teeth from below; *b*, right mandibular ramus from above. From the John Day river of Oregon. Original.

the form of the inferior sectorial tooth. In *Oligobunis* it has the primitive form seen in most of the Miocene species, while according to Flower, in *Icticyon* there is no internal cusp, and

there is a cutting heel. The number of true molars, $\frac{1}{2}$, is the smallest in the family. A single species is known, the *O. crassivultus* Cope, from the John Day bed of Oregon. The skull is about the size of that of the wolverene (*Gulo luscus*), and is of robust form. The canine teeth are powerfully developed, and indicate an animal of strong predaceous instincts.

GENERAL OBSERVATIONS.

The succession of these genera, as indicated by their structure, is as follows:



This order is not entirely that of succession in time. Thus Megalotis, which represents the primitive type of all Canidæ, is only known as living, and the *Megalotis zerda* is African. We anticipate its discovery in a fossil state. Amphicyon and Galecynus are the oldest known Canidæ, as they characterize the lowest Miocene, and probably the Upper Eocene epochs, Canis appears next in time in Europe, probably in the Middle Miocene. In America the genera of the John Day Middle Miocene precede Canis. I refer to Temnocyon, Enhydrocyon, Hyæncyon and Oligobunis, which were contemporaries. Ælurodon appeared later than Canis in the Upper Miocene and Loup Fork, and Dysodus and Icticyon with various other genera not here enumerated, are recent. Canis is the prevalent genus in the present period, as Galecynus was during the Miocenes. That the last named genus, with its numerous species, has given origin to the existing species of Canis, as suggested by Filhol, is altogether probable.

As already mentioned, the successional change in the Canidæ has been exhibited in the reduction of the numbers of the tubercular teeth. To this may be added a successive increase in the size of the sectorials and canines. In these points the Canidæ

epitomize the history of the evolution of the dentition of the order of Carnivora. This I stated as follows, at a meeting of the Philadelphia Academy of Feb. 16, 1875:¹ "The important change [in the Carnivora] which is clearly indicated, is the progressive extinction of the genera with numerous sectorial teeth, accompanying the increasing specialization of those which remain. In other words the numerous types of digitigrade Carnivora which have survived, are those developing one sectorial tooth (whose earliest representative is *Didymictis*). The increased perfection of the sectorial has been associated with a reduction in the number of the other molars, first posterior, then anterior to it, which reduction has been accompanied by an increased relative size of the sectorial." These views were extended in a paper on "The Origin of the Specialized Teeth of the Carnivora," in the *AMERICAN NATURALIST* for March, 1879. In a paper published in the Proceedings of the Zoölogical Society of London, August, 1880, Professor Huxley comes to the same conclusion that I have stated in the above papers, in apparent ignorance of their prior publication.

As regards the origin of the Canidæ, it is doubtless to be found among the forms of the Creodonta.² The Creodonta are flesh-eaters of various degrees of power, without scapholunar bone; with well defined canine teeth; with a low type of brain, and generally imperfect ankle-joint. They stand in nearest relation to the Insectivora, but have points of resemblance to the Marsupialia. I originally included them as a sub-division of the Insectivora,³ but subsequently placed them with the Insectivora and several other sub-orders in a comprehensive order, which I termed the Bunotheria.⁴ This view of the origin of the Carnivora was subsequently reaffirmed by Huxley in his paper of 1880, above cited. He reproduces all my evidence, and in some cases almost my language, but is evidently unacquainted with the previously existing literature.

I have indicated the Miacidæ as the probable parental stock of the Canidæ among the Creodonta.⁵ They are the only members

¹Proceedings, p. 22.

²See Report U. S. Geol. Survey W. of 100th mer. G. M. Wheeler, 1877, II, p. 282.

³Proceedings Academy Philada., 1875, Nov., p. 447.

⁴See Report Capt. Wheeler, 1877, IV, p. 85.

⁵On the genera of the Creodonta, Proceed. Amer. Philos. Soc., 1880, p. 81.

of the sub-order which exhibit the true sectorial tooth of the upper series, as it exists in the Carnivora, and the genus *Didymictis* has the dental formula of *Canis* above. *Miacis* has the formula of *Canis* below, but that of the superior series is unknown. It would not be surprising if it should turn out to be that of *Amphicyon*. These animals are abundant in the Middle and Lower Eocenes of North America.

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"THE PLAINS" OF MICHIGAN.

BY PROFESSOR V. M. SPALDING.

IN the northern central portion of the lower peninsula of Michigan there extend through several counties large tracts designated on some of the maps as "barrens," but uniformly spoken of as "the plains" by people living upon them or in their vicinity. One of these tracts, perhaps the most extensive, lies along the line of the Mackinaw division of the Michigan Central railroad and occupies a large portion of Crawford county, extending into the adjacent counties on the east side and south, and including an area of over a thousand square miles. A similar, though somewhat less extensive, region of barrens or plains is intersected by the Flint and Pere Marquette railroad, having its center in Lake county, extending southward into Newaygo and northward as far as the Manistee river. Similar plains, of greater or less extent, are to be found in this part of the State and in the northern peninsula, but the two tracts already mentioned may be taken as fair representatives.

These plains lie in what is known as the "pine belt" of Michigan, and include the poorest portions of this extensive region. Their soil is a light sand, so fine that it penetrates one's shoes as he walks over it, and when a handful is closely examined it is seen to consist almost wholly of fine grains of silica, "good to make glass of," as is remarked by those of the inhabitants who do not believe in its agricultural capabilities. Nevertheless, these plains are by no means a desert. They support quite a variety of vegetable life, and one experiences no feeling of loneliness as he travels over them. On the contrary, wherever they have escaped the destructive action of fire, the smooth, gently undulating ground, with its groves of scrub pine, through which the eye has an extended range in every direction, produces a pleasing impres-